

SPECIES RICHNESS AND TURNOVER OF ANTS (FORMICIDAE) ALONG  
AN ALTITUDINAL GRADIENT (GIRÓN – PARAMO OF BERLÍN),  
SANTANDER COLOMBIA.

ERIKA YOLANDA AMAYA MEJIA

UNIVERSIDAD INDUSTRIAL DE SANTANDER  
FACULTAD DE CIENCIAS  
ESCUELA DE BIOLOGÍA  
BUCARAMANGA

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ERIKA YOLANDA AMAYA MEJIA

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Biólogo

Director

Victor Hugo Serrano Cardoso

Profesor UIS

UNIVERSIDAD INDUSTRIAL DE SANTANDER

FACULTAD DE CIENCIAS

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**AUTOR:** Erika Yolanda Amaya Mejía \*\*

**PALABRAS CLAVES:** hormigas, clima, gradiente elevacional, riqueza de especies, efecto del dominio medio.

### Resumen:

El objetivo de este estudio fue estudiar el patrón de riqueza y el recambio de hormigas en un transecto elevacional. Exploramos si la riqueza de especies a lo largo del gradiente está relacionada con variables climáticas, medioambientales y/o el efecto del dominio medio. El estudio se realizó desde Girón al Páramo de Berlín, el cual tiene un gradiente elevacional que va de 710 a 3318 m.s.n.m. en Santander, Colombia. El muestreo se realizó entre Julio de 2007 y Enero de 2008. Diez sitios fueron muestreados, los cuales fueron localizados a intervalos de 250 m.s.n.m. El Modelo Autorregresivo Condicional (CAR) fue usado para examinar el efecto de los factores climáticos, medioambientales y las predicciones del modelo nulo del dominio medio sobre la riqueza de especies. 113 especies y 7 subfamilias fueron colectadas e identificadas. El recambio de especies y la similaridad entre faunas mostró un alto reemplazo de especies que aumenta con la elevación. Un uniforme decline en la riqueza de especies se encontró con la elevación después de los 1000 m.s.n.m. La riqueza de especies está relacionada positivamente con la temperatura y el porcentaje de transmitancia cuando todas las especies y las especies de rangos largos fueron analizadas. Las especies de rangos cortos, mostraron correlación con la heterogeneidad vertical de la vegetación y el número de árboles. Sin embargo, el factor geométrico no contribuye, en ninguno de los casos, a la variación en la riqueza de especies.

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\*Trabajo de investigación

\*\*Facultad de Ciencias, Escuela de Biología, Director: Víctor Hugo Serrano Cardozo

## ABSTRACT

**TITLE:** SPECIES RICHNESS AND TURNOVER OF ANTS (FORMICIDAE) ALONG AN ALTITUDINAL GRADIENT (GIRÓN – PARAMO OF BERLÍN), SANTANDER COLOMBIA.\*

**AUTHOR:** Erika Yolanda Amaya Mejía \*\*

**KEY WORDS:** Ants, climate, elevation gradient, species richness, mid-domain effect

### **Abstract:**

The richness patterns and turnover of ants was studied along an elevation transect. It was explored as to whether ant species richness along the gradient is related to climatic and environmental variables. The study was carried out in Girón – Paramo of Berlín which has an elevational gradient ranging from 710 to 3318 m a.s.l. in Santander, Colombia. Sampling was carried out between July 2007 and January 2008. Ten sites were sampled, which were chosen at 250 m a.s.l. intervals. Conditional Autoregressive model (CAR) was used to examine the effects of climatic, environmental and mid-domain null model predictions factors on ant species richness. 113 species and 7 subfamilies were collected and identified. Species turnover and faunal similarity measures showed a high species replacement that increase with elevation. A uniform decline in species richness was found with elevation after the 1000 m a.s.l. The species richness is related positively with temperature and percentage of transmittance when all species and large-range species were analyzed. Small-range species showed correlation with the vertical heterogeneity of the vegetation and the number of trees. However, the geometric factors do not contribute, in neither case, to the variation in species richness.

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\*Research

\*\* Facultad de Ciencias, Escuela de Biología, Director: Victor Hugo Serrano Cardozo

## 1. INTRODUCTION

Understanding the patterns and the geographical variational causes of the diversity is a principal objective of ecology. Most of the studies made in animals (e.g., Gaston 2000, Jetz & Rahbek 2001, McCain 2003) and plants (e.g., Ellison 2002) have showed a peak of richness in low latitudes and decrease towards the poles. Along elevation gradients, especially in those which are placed within the inter-tropical zones, two richness patterns have been reported, a monotonic decrease (e.g., Brown 1973, Fisher 1996, Brühl *et al.* 1999) and a hump-shaped (e.g., McCoy 1990, Rahbek 1995, Escobar *et al.* 2005). Many climatic, ecological and historical explanations have been proposed to understand these geographical variations in species richness; however these subjacent mechanisms are still poorly explored (Rahbek 1995, 1997, Lomolino 2001, Hawkins *et al.* 2003).

In addition to the contemporary environmental explanations, Colwell and Hurtt (1994) and Willig and Lyons (1998) proposed to evaluate the null hypothesis in which the geographical ranges are placed at random, geometrical constrains along the domain. This effect is normally named the Null Model of the Mid-domain Effect (MDE). Its predictions are shown by a hump-shaped diversity curve, which arises from a greater overlap of species in the mid-elevation than the lower and higher elevations (Brehm *et al.* 2007).

With ants as in other insect groups, the distribution patterns in altitudinal gradients do not follow strict laws. Studies in gradients of many places have been made to determine these patterns. It has been observed that the relationship between the richness and the altitude is inverse; in fact, less species were found at high elevations in Malaysia (Brühl *et al.* 1999), United States (North Caroline, Sanders *et al.* 2003), Venezuela (Janzen *et al.* 1976) and Madagascar (Fisher 1996). In the case of Panama (Olson 1994), Philippines (Samson *et al.* 1997), and United States (Nevada, Sanders *et al.* 2003), richness is greatest in the intermediate zones of the gradient. Besides, it has been found that there are no species of ants above certain altitudes; Brown

(1973) did not find ants above 2300 m a.s.l., and Brühl *et al.* (1999) and Janzen (1973, 1976) confirmed this but at different altitudes, above 2600, 2800 and 3550 m a.s.l. respectively.

The influence of environmental variables in the described distribution patterns was not analyzed in those studies but the authors postulated that temperature and humidity are related to the richness of ants. In the upper altitudinal border where there are daily low temperatures, cloud cover, reduced radiation and high humidity, the soil is constantly saturated with water (Brühl *et al.* 1999). These characteristics lead to a drastic decrease of ant species, because the foraging time is short resulting in difficulty supporting the colony (Janzen 1973, Olson 1994, Fisher 1996).

In altitudinal gradients of the tropical region, ant species have small distribution ranges, as occurs in most species of these zones, which have greater specificity for habitat and narrow tolerance of ranges in the environmental conditions (Janzen *et al.* 1976, Stevens 1989, Brühl *et al.* 1999). The previous characteristics mean that the ant composition changes rapidly along the gradient, as has been observed in the Kinabalu Mont in the north of Malaysia (Brühl *et al.* 1999), where the species changed by more than 50% between two adjacent sites. However, the species turnover is inversely related with elevation, being higher in the low zones where the result is due to the loss of species (McCoy 1990, Fisher 1996).

Ants have been used as model organisms to understand the mechanisms responsible in the composition of the wet tropical forest communities thanks to their ubiquity, domain and easy experimental manipulation (Levings & Franks 1982, Andersen 1990). They are one of the most important insect groups in the forest in terms of biomass, number of individuals and ecological impact (Fittkau & Klinge 1973, Basu 1997). Ants have many functions in the ecosystem. Firstly, the remotion and enrichment of the soil. Large colonies of ants can excavate many meters of soil, aerating and incorporating surface residues. Secondly, seed transportation which allows plants to colonize new areas and protecting seeds from depredation. Thirdly, as potential pollinators. Though there are few

plants species that are pollinated by ants; most ant species have agents that can attack pollen or do not have differentiated hairs that allow them to transport seeds (Carroll & Janzen 1973, Fernandez 2003).

## **2. METHODS**

### **2.1. Study area**

The study was carried out on the west flank of the Cordillera Oriental of the Colombian Andes, in the Santander state. The samples were taken along an elevational transect between 708 and 3318 m a.s.l during 2007 and 2008. Ten sampling sites along the elevational transect were surveyed: 708, 1000, 1188, 1486, 1710, 1896, 2295, 2484, 2850 and 3318 m. All sampling sites chosen depended on logistical suitability and zone security. We surveyed two temporal replicates at the original ten elevation sites: dry season (July to September 2007) and wet season (October 2007 to January 2008).

### **2.2. Sampling**

Trapping was a combination of pitfall and bait traps at each site. The pitfall traps were constructed with plastic glasses (7 oz). Each one was partially filled with water and soap following Fernandez (2003). These traps were embedded so that the lip of the cup was flush with the soil surface. They were retrieved 48 hours after being activated. The bait traps (Tuna in oil and peanut butter) were of two types: epigeous and arboreous. These traps were built with paper of 13 cm x 4 cm, in the center was put the respective bait and it was folded. The epigeous traps were put on the soil surface and the arboreous traps were put at 2 m from the ground, in the trees. After 2 h the traps were reviewed and these were put again at the next day using the same methodology.

At each site traps were 10 m apart and perpendicular to the elevational transect. Each transect has 440 m long, with 15 pitfall traps, 60 bait traps (divided equitably in 4 groups per bait type and location) at each day. A total of 135 traps were placed for sample site. Traps were put in the following order, first a pitfall trap; second the traps with tuna in oil (one arborea and one epigea) and finally, the traps with peanut butter bait. This series was repeated 15 times in each one of the sample sites. Additionally, it was collected a sample of litter of a quadricle of 50 x 50 cm in each one of the sites. Ants were obtained using

the Berlesse funnel. Specimens were identified to genera using keys of Bolton (1997) and Fernández (2003). Voucher specimens were deposited in the arthropod collection of the Museo de Historia Natural of the Universidad Industrial de Santander and copies in the Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

### **2.3. Analyses**

We used species accumulation curves to assess how well species diversity was sampled for each of the ten evaluated locations. Additionally, true species richness for each site was also estimated using Chao 2, a non-parametric, incidence-based richness estimator. The EstimateS Version 7.5 software (Colwell 2005) was employed to generate the smoothed species accumulation curves and the estimators of true species richness. In addition, this software was used to compute Chao's incidence-based Sørensen Index. This index reduces undersampling bias by estimating the effect of unseen, species shared. It is based on the probability that two randomly chosen individuals, one from each of two samples, both belong to species shared by both sites (not necessarily the same shared species) (Chao *et al.* 2004). Species turnover between elevations was calculated in two ways. First, beta diversity proposed by Whittaker (1960) was used. Also, we calculated beta diversity developed by Lennon *et al.* (2001), because this measure distinguishes between species turnover and the loss of species along the gradient without adding new species (Koleff *et al.* 2003).

The potential effects were considered on species richness at ten sites of two climate variables (annual mean temperature and annual precipitation), seven microhabitat variables (percentage of transmittance, soil humidity, horizontal and vertical heterogeneity of the vegetation, canopy height, DAP and number tree) and geometric constraints (mid-domain effect). Unfortunately, because data from permanent weather stations in transect were no available, we obtained for each one of the sample sites the data of climatic base of DIVA-GIS (Hijmans *et al.* 2004). We took a photograph of canopy at 50 cm from the soil; the photographs were imported into Winphot 5.0 software (Steege 1996) and

the total transmittance percentages were calculated for each image. DAP and the numbers of trees were calculated for trees with greater than 16 cm perimeter.

We used RANGEMODEL software, ver. 5 (Colwell 2006) to estimate predicted richness under the influence of the mid-domain effect by randomizing the placement of the complete set of empirical ranges along the gradient, under the geometric constraint the no range may extend beyond the limits of the domain. In this case, we used the discrete null model developed for Dunn *et al.* (2006), which maintain the observed range sizes and occupancies, the gaps in observed distributions were no filled by “interpolation” between the most distant sampling points at which each species was recorded along the domain. In this model, sampling points along the domain are treated as ordered, evenly spaced, discrete bins. We carried out range randomizations for the full dataset. Mid-domain effect theory indicates that species with large-ranges are more likely to mid-domain richness peaks more pronounced than species with smaller-ranges (Colwell *et al.* 2004). To assess this prediction, we considered a species to have a small-range if it was recorded an only one site, whereas any species recorded at two or more sites was considered to have a large-range. For the full dataset and for the two range-size subset for each river, we repeated the resampling 5000 times and estimated 95% confidence intervals for the pattern of species richness.

To assess the statistical relationship between species richness and its potential predictors (Annual mean temperature, annual precipitation, percentage of transmittance, soil humidity, horizontal and vertical heterogeneity of the vegetation, canopy height, DAP, number tree and geometric constraints) we used CAR (Conditional Autoregressive model), relying on Akaike Information Criterion (AIC), as implemented in SAM (Rangel *et al.* 2005), additionally, to select the best model. We calculated  $\Delta_i$ , the best model have  $\Delta = 0$ , while the rest of the models have positive values.  $\Delta_i \leq 2$  have substantial support, those where  $4 \leq \Delta_i \leq 7$  that have considerably less support and models having  $\Delta_i \leq 10$  have essentially no support (Burnham and Anderson 2002). We implemented the methodology proposed by Dunn *et al.* (2006) for model selection algorithm.

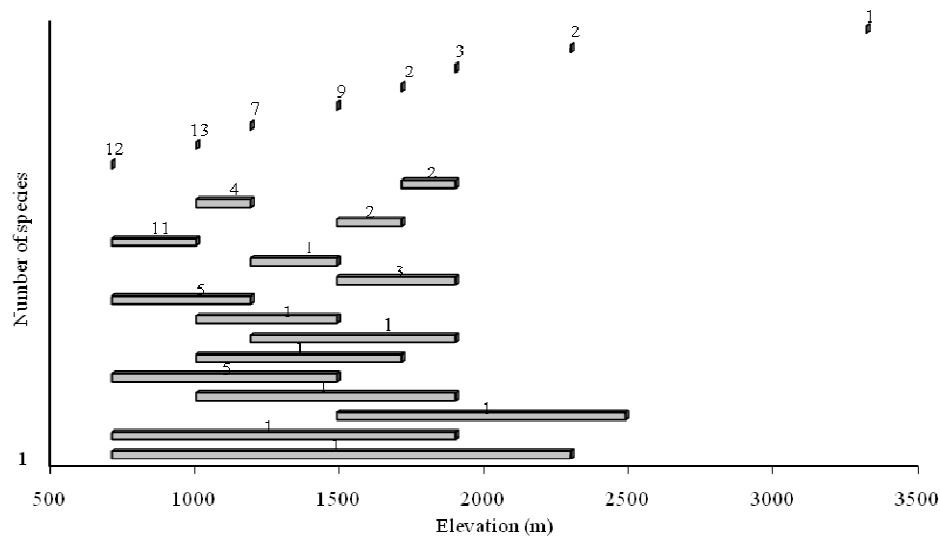
First, we carried our CAR for all single-variable models and selected the model with the minimum AIC ( $\Delta = 0$ ). Second, we explored all two-variables models that included the variable selected in the first step and chose the model with the minimum AIC ( $\Delta = 0$  or  $\Delta_i \leq 2$ ). We then repeat the procedure for all three-variable models that included the two previously selected, and so on, until AIC could not be further reduced. We log-transformed all variables; except percentage of transmittance, which was transformed with  $\text{Cos}(x \cdot 100)^{1/2}$  to normalize the distribution and reduce the effect of outliers.

### 3. RESULTS

At 10 sites along the elevational gradient, we detected 113 morphospecies of which 58 (51%) were identified to named species (Table 1). Of these morphospecies, 51 were assigned to the subfamily Myrmicinae, they constitute nearly half of the species recorded (45%), 21 to the subfamily Formicinae, 13 to the subfamily Dolichoderinae, and the remainder to five other subfamilies (Ponerinae, Pseudomyrmecinae, Ectatomminae, Ecitoninae). In Twenty one percent out of all species gaps in their distributions were observed. A full list is provided in Appendix 1. Moreover, the distribution of species by site shows that about half (44%) of species occur at only one site, whereas 22 % were recorded in only two sites and none of the species was found in the ten sites (Figure 1). The proportion of species recorded progressively decreases with increasing range size.

**Table 1.** Ants at ten elevations along the gradient. The first three columns show the number of ants species, genera and subfamilies identified at each study site along the gradient. The last column shows the richness estimation using Chao 2 (the numbers in parentheses represent the percentage estimated species that were recorded).

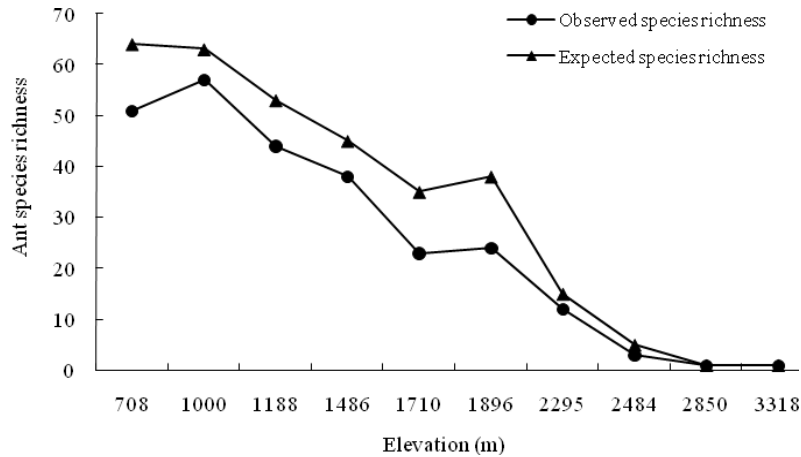
Elevation (m)	Species	Genera	Subfamilies	Chao 2
704	51	22	6	64 (84%)
1000	57	23	7	63 (90%)
1188	44	22	7	53 (83%)
1486	38	19	7	45 (84%)
1710	23	15	6	35 (66%)
1876	24	13	5	38 (63%)
2295	12	6	4	15 (80%)
2484	3	3	3	5 (60%)
2850	1	1	1	1 (100%)
3318	1	1	1	1 (100%)
Pooled elevations	113	37	7	



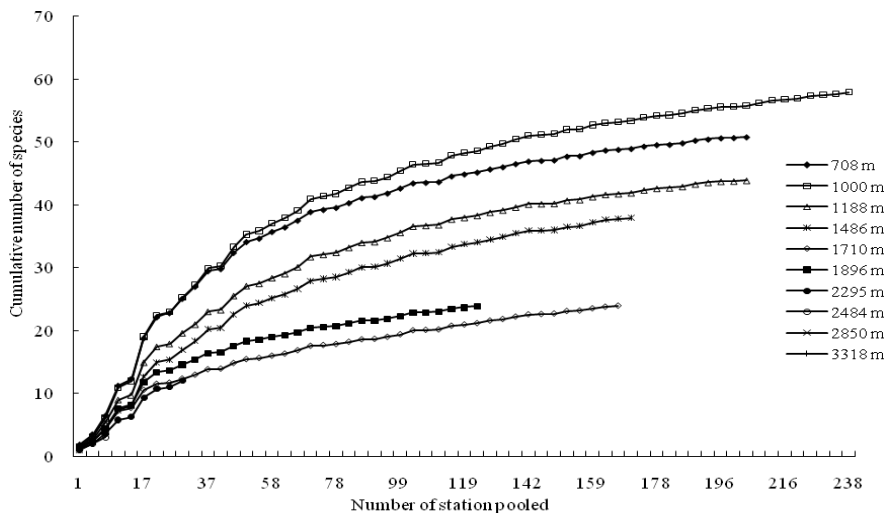
**Figure 1.** The number of species in each altitudinal range category for all tabulated species of continuous range. The actual number of species is given to over the category block.

Ants species richness decreases rapidly towards the end of the gradient elevation. However, observed richness show a peak of richness in 1000 m, while expected richness has species maxima at 704 m (Figure 2). Most species-accumulation curves at each elevational site reached a plateau in species richness before the end of the survey period. In two sites did not plateau, 2484 m and 2850 m (Figure 3). Species richness estimator Chao 2 demonstrated the same overall pattern of species richness, although as expected, Chao 2 estimated greater minimum species richness than was actually observed at each elevation (Table 1).

Faunal similarity values based on Chao's incidence-based Sørensen index were high between sites within 200 m elevation of each other but decrease with increasing difference in elevation between sites (Figure 4). Moreover, the estimator for the index (open circles) has a greater value than the corresponding raw index value (asterisk). These differences were greater for ants communities at nearby elevations.

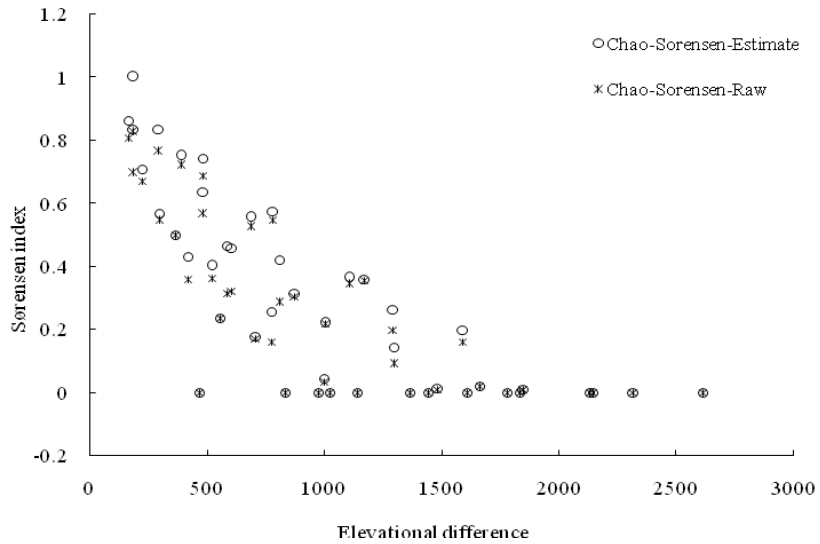


**Figure 2.** Ant species richness along the elevational transect. Observed species richness (▲) and Expected species richness (●) with Chao 2 .



**Figure 3.** Species-accumulation curves for observed ants at each elevational study site along the Bucaramanga – Paramo of Berlín (Colombia) elevational gradient.

$\beta_W$  and  $\beta_{SIM}$  values showed similar trends in species turnover between elevations. There is a direct relationship between the species turnover and elevation. The turnover was lower in lowest elevations, for example, between 708 and 1000 m and 1000 y 1188 m (Table 2). However,  $\beta_{SIM}$  values of five pairs of altitudinal sites indicate that there is not species turnover, contrary to what shown by the high values of  $\beta_W$ .



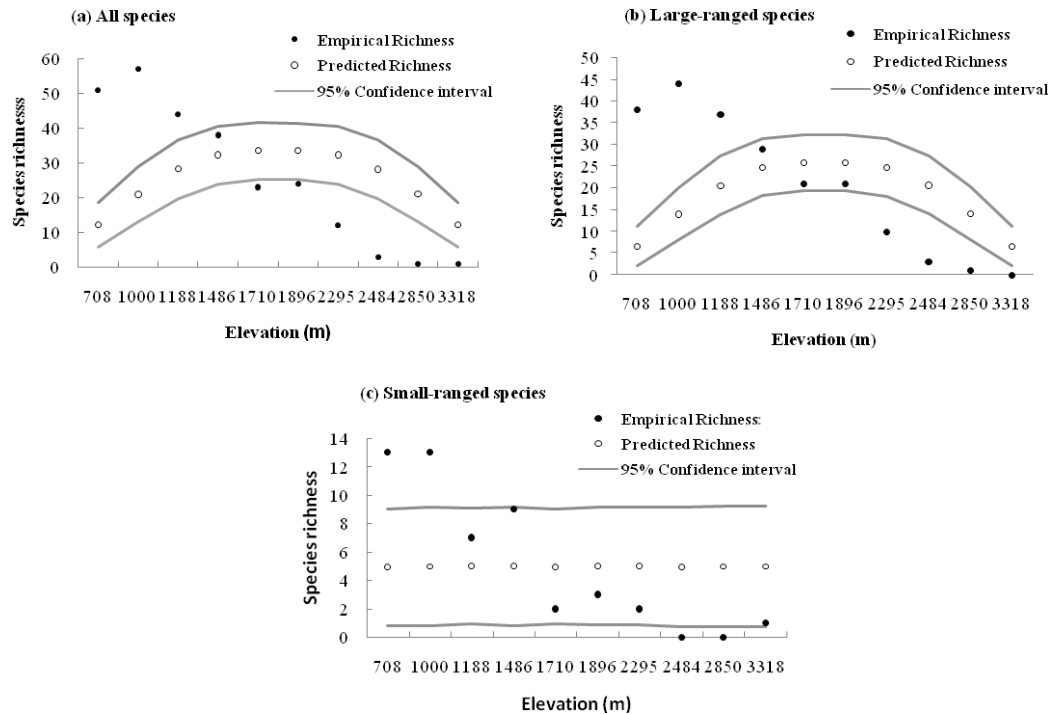
**Figure 4.** Ant community similarity as a function of elevational difference between sites. Chao-Sørensen index estimator (○) and raw Chao-Sørensen index (\*).

**Table 2.**  $\beta_W$  (above the diagonal) and  $\beta_{SIM}$  (below the diagonal) diversity values of each pair of altitude sites. Bold values represent comparisons of altitudinally adjacent samples.

Elevation	708	1000	1188	1486	1710	1896	2295	2484	2850	3318
708	—	<b>0.353</b>	0.500	0.605	0.739	0.667	0.500	1	1	1
1000	<b>0.389</b>	—	<b>0.364</b>	0.500	0.739	0.625	0.417	0.667	0	1
1188	0.532	<b>0.446</b>	—	<b>0.553</b>	0.545	0.500	0.417	0.333	0	1
1486	0.663	0.600	<b>0.585</b>	—	<b>0.435</b>	0.458	0.500	0.667	1	1
1710	0.838	0.850	0.697	<b>0.574</b>	—	<b>0.417</b>	0.583	0.333	1	1
1896	0.784	0.778	0.647	0.581	<b>0.404</b>	—	<b>0.667</b>	0.333	1	1
2295	0.810	0.797	0.750	0.760	0.714	<b>0.778</b>	—	<b>0</b>	0	1
2484	1	0.967	0.915	0.951	0.846	0.852	<b>0.6</b>	—	<b>0</b>	1
2850	1	0.966	0.956	1	1	1	0.846	<b>0.5</b>	—	<b>1</b>
3318	1	1	1	1	1	1	1	1	<b>1</b>	—

Figure 5 shows MDE model predictions generated with observed distribution ranges and randomized range placement. Large ranges were defined as ranges of greater than one site, while small ranges were those limited to one site.

Observed species richness is always higher than predicted richness at the first two or three sites of the gradient, and tends to be lower at the end of gradient. In the most individual sites, the observed richness did not fall within the 95% confidence limits. The pattern of all species is reflected by large-ranged species, which dominate the information in the pattern for all species (Figure 5a-b).



**Figure 5.** Empirical species richness (solid points), predicted species richness (open points; the computed means of 1000 mid-domain effect randomizations) and 95% confidence intervals for the MDE richness predictions as a function of elevation for each data set. (a) for all species-range, (b) large ranges and (c) small ranges.

We detected that the results for Conditional Autoregressive (CAR) model depended upon the size of the species range (Table 3). When all species and large-ranged species were analyzed, the first explanatory variable to enter the autoregression model and explaining 94% of the variation in richness was annual mean temperature, followed by percentage light transmittance with a smaller explanatory contribution, 2% (The upper portion of Table 3). In the final (best) model when small-range species were considered two variables entered too, vertical heterogeneity (explaining 77% of the variation in richness) and

number of trees. These variables were positively associated with richness (The lower portion of Table 3)

**Table 3.** Results of CAR of observed richness over the Girón-Berlín transect as a function of environmental variables and MDE predictions. To model selection algorithm see text. Variables that entered each model are numbered in order of entry. Slope is the standardized partial regression slope of the variable in the best model.  $R^2$ , for the numbered variables, is the increase in total variance explained as each variable entered the mode; and for the final (best) model, is the total explained variance for each final model. AICc is the Akaike Information Criterion for each model.

Model		All species	Large ranges	Small ranges
Var. Selected				
1. Annual mean temperature	Slope	6.816	6.275	
	$R^2$	0.936	0.977	
	AICc	22.491	12.605	
2. Percentage light transmittance	Slope	6.352	4.284	
	$R^2$	0.021	0.019	
	AICc	15.971	2.946	
Final model	$R^2$	0.957	0.996	
	AICc	15.971	2.946	
1. Vertical heterogeneity	Slope			3.963
	$R^2$			0.766
	AICc			29.799
2. Number of three	Slope			-1.386
	$R^2$			0.158
	AICc			27.537
Final model	$R^2$			0.924
	AICc			27.537

#### 4. DISCUSSION

The species richness estimator Chao 2 and observed species accumulation curves indicated that the species richness along the gradient were sampled effectively at each study elevation, with a richness estimated between 60 and 100 % of the true species richness (Figure 3, Table 1). These results are similar to those observed in others studies in tropical biotas, which have reported unsaturated species accumulation curves because they have high species richness (e.g. Fisher 1996, Longino *et al.* 2002). Thus, some species of ant remain to be identified in the sampling sites, judging by the curves of accumulation of species has not reached the asymptotic. Of the ants species studied here, 24% had an altitudinal range discontinuous. Of the remaining species, 44% of species occurred only at a single locality.

Observed species richness shows that the 1000 m site is higher species richness, whereas richness estimators (Chao 2) for each elevation demonstrate that the highest species richness is on the 708 m site. In both case, 2850 m and 3318 m sites have the smallest species richness, i.e. altitudinal pattern of species richness shows a monotonic decline (Figure 2, Table 1). This pattern has been observed in several altitudinal studies of tropical ant communities (e.g. Brühl *et al.* 1999, Fisher 2002). However, another model has also been reported, mid-domain peak in species richness (e.g. Olson 1994, Fisher 1996, Samson *et al.* 1997). Of those studies that found a peak in ant species richness, the greatest richness occurred at elevations between 700 and 1000 m. Since in our study the elevational gradient has no sites lower than 700 m, the mid-elevation peak can not be detected.

$\beta_W$  and  $\beta_{SIM}$  indices differ because:  $\beta_W$  depends of the level of continuity in the species composition between the two quadrants observed, while  $\beta_{SIM}$  consider the replacement or species loss, since it focuses on differences in composition rather than on differences in species richness (Koleff *et al.* 2003). Species turnover increased as elevation increased, nevertheless, species replacement is most prevalent at the lowest elevations. For example, between 708 and 1000 m the measured species turnover is the result of the difference in species and

not a loss of species at 1000 m. Contrary to what is seen at high elevations, where there is loss of species without replacement. However, there are several pairs of  $\beta_{\text{SIM}}$  values at high elevations with minimum values indicating that there was no loss of species between the two sites, contrary to what is expected. For example, between 2484 and 2850 m there is a loss of nine species at 2850 m, although the index reports to the contrary, this may be caused because the three species reported in the second site are also in the first site.

The results found with the indices of beta diversity are consistent with Chao's incidence-based Sørensen index, which shows that there is a decline in the similarity to increase the elevation difference (Figure 4). The estimator index values show more similarities to the corresponding values of the raw index values. These differences are greater in nearby elevations, which can be expected because it is more likely to have more undetected species in common than ants communities at distant elevations (Cardelús *et al.* 2006).

In recent years, several studies have taken into account MDE null models with potential explanations for patterns of species richness along a variety of domains (Colwell *et al.* 2004). In these studies generally the ranges within domain are treated as if they were continuous, using the interpolated richness. Nonetheless, the use of interpolated richness tends to underestimate severely the species richness at the extremes of the gradient and overestimate species richness in the middle of the gradient, which might cause amplified or even create mid-domain peaks in richness (Grytnes & Vetaas 2002). For this reason, we used the discrete null model (see methodology). We found that observed species richness, regardless of range size, does not fall within the 95% confidence limits at most individual sites (Figure 5). Therefore, at least for ants in this study, species richness is more correlated with environmental variables than with the MDE null model (see below).

Patterns of species richness ants in elevational gradients have a multiplicity of explanations, without reaching a consensus (Brühl *et al.* 1999, Kaspari *et al.* 2000). In our study, the results of CAR suggest that a combination of environment and climatic factors may affect the richness patterns of ants, rather

then a single factor. However, this combination of factors depends of the size of the species ranges. Annual mean temperature is strongly correlated with richness of all-species as well as with large-range species, followed with a smaller explanatory contribution of light percentage transmittance. On the other hand, vertical heterogeneity and number of trees are strongly correlated with small-range species.

Temperature may affect the ants species richness directly or indirectly. Indirectly, temperature affects productivity, and this in turn influences the species richness through two relationships, the net primary productivity (NPP) limits a taxon's density, and taxon density limits species richness. Greater availability of energy in the habitat increases the number of individuals who can withstand the environment, as well as population size, decreasing the rate of extinction (Kaspari *et al.*, 2000). Directly, temperature may affect of two forms. First, temperature is important for foraging. The foraging activity tends to occur in a range that starts at 10 °C, has its maximum 32.3 °C and finish to 40.6 °C (Hölldobler & Wilson 1990). High temperatures can increase the activity of individuals within the colonies, making these go find food and thus increase the resources for maintaining the colony (Dunn *et al.* 2006). Second, low temperatures can reduce important metabolic processes and impede or prevent the development of eggs and larvae (Brown 1973). The positive correlation between species richness and vegetation cover is seen through the mayor availability of resources for the ants through the production from the plants (Hawkins *et al.* 2003).

Small-range species are correlated with spatial heterogeneity (vertical heterogeneity and number of trees). The greater habitat heterogeneity, the more subdivisions the habitat contains (i.e. microhabitats) and more species can co-exist (Pianka 1966). These small-range species may be ecological specialists, may tolerate only a limited range of habitats. Thus, some studies have found that species with narrow geographical ranges are likely to experience a reduce range of conditions and have narrow environmental tolerance (Quinn *et al.* 1997). However, this conclusion remains speculative as long as no further analyses are made.

In summary, it has been found that the species richness of ants along the gradient “Girón - Paramo of Belín” is affected by climatic and environmental conditions. However, these relations depend of the size range. For large-range species, the temperature is the most important variable that determinate the richness pattern. And, for small-range species the variable most important is habitat heterogeneity. Moreover, mid-domain models predicted not only were wrong when we considered all species, but also when we divided dataset in species with the largest ranges and species with the smallest ranges.

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## 6. APPENDIX

**Appendix 1.** The elevation ranges of ants species recovered in the gradient altitudinal Girón – Páramo de Berlín, Santander Colombia.

Species	Elevational range									
	708	1000	1188	1486	1710	1896	2295	2484	2850	3318
<b>Dolichoderinae</b>										
<i>Azteca sp. 1</i>	■	■								
<i>Azteca sp. 2</i>	■	■								
<i>Azteca sp. 3</i>	■									
<i>Azteca sp. 4</i>		■	■							
<i>Azteca sp. 5</i>		■								
<i>Azteca sp. 6</i>				■						
<i>Dolichoderus sp.</i>		■								
<i>Dorymyrmex pyramicus</i>			■							
<i>Linepithema sp. 1</i>			■							
<i>Linepithema sp. 2</i>			■	■						
<i>Linepithema sp. 3</i>				■						
<i>Linepithema sp. 4</i>					■					
<i>Tapinoma melanocephalum</i>	■									
<b>Ecitoninae</b>										
<i>Eciton burchellii</i>						■				
<i>Labidus coecus</i>		■	■				■	■	■	
<i>Labidus praedator</i>				■	■					
<b>Ectatomminae</b>										
<i>Ectatomma confine</i>		■	■							
<i>Ectatomma ruidum</i>	■	■	■	■						
<i>Ectatomma tuberculatum</i>		■								
<i>Gnamptogenys andina</i>			■	■	■	■				
<i>Gnamptogenys bispinosa</i>					■	■				
<i>Gnamptogenys strigata</i>				■	■	■				
<b>Formicinae</b>										

<i>Brachymyrmex</i> sp. 1	■								
<i>Brachymyrmex</i> sp. 2		■							
<i>Brachymyrmex</i> sp. 3		■	■			■			
<i>Camponotus linnaei</i>		■	■	■	■	■			
<i>Camponotus</i> sp. 1		■		■					
<i>Camponotus</i> sp. 2	■								
<i>Camponotus</i> sp. 3	■	■	■						
<i>Camponotus</i> sp. 4				■					
<i>Camponotus</i> sp. 5			■						
<i>Camponotus</i> sp. 6	■								
<i>Camponotus</i> sp. 7	■								
<i>Camponotus</i> sp. 8	■	■							
<i>Camponotus</i> sp. 9		■							
<i>Camponotus</i> sp. 10			■						
<i>Camponotus</i> sp. 11	■	■	■						
<i>Camponotus</i> sp. 12	■	■	■	■			■		
<i>Camponotus</i> sp. 13	■	■							
<i>Paratrechina caeciliae</i>	■	■	■	■					
<i>Paratrechina longicornis</i>	■	■							
<i>Paratrechina</i> sp. 1		■							
<i>Paratrechina</i> sp. 2					■				
<b>Myrmicinae</b>									
<i>Acromyrmex</i> sp.	■	■							
<i>Acromyrmex</i> sp.				■					
<i>Atta cephalotes</i>	■	■							
<i>Cardiocondyla emeryi</i>	■	■							
<i>Cardiocondyla nuda</i>	■								
<i>Cephalotes</i> - Undescribed species						■			
<i>Cephalotes clypeatus</i>	■	■							
<i>Cephalotes grandinosus</i>		■							
<i>Cephalotes minutus</i>			■						
<i>Cephalotes umbraculatus</i>		■							
<i>Crematogaster curvispinosa</i>	■	■	■	■					

<i>Creumatogaster distans</i>	■	■	■							
<i>Creumatogaster erecta</i>	■	■	■							
<i>Creumatogaster longispina</i>					■	■				
<i>Creumatogaster nigropilosa</i>		■	■	■	■					
<i>Creumatogaster torosa</i>		■								
<i>Cyphomyrmex major</i>	■				■	■				
<i>Eurhopalothrix sp.</i>						■				
<i>Megalomyrmex sp.</i>				■	■					
<i>Monomorium floricola</i>	■									
<i>Mycocepurus smithii</i>	■									
<i>Octostruma sp.</i>			■		■	■				
<i>Pheidole sp. 1</i>				■	■	■				
<i>Pheidole sp. 2</i>	■	■	■	■	■	■				
<i>Pheidole sp. 3</i>	■	■	■	■	■	■	■			
<i>Pheidole sp. 4</i>	■	■		■		■				
<i>Pheidole sp. 5</i>	■	■		■		■				
<i>Pheidole sp. 6</i>	■	■	■	■		■				
<i>Pheidole sp. 7</i>	■	■	■			■	■			
<i>Pheidole sp. 8</i>	■	■	■			■				
<i>Pheidole sp. 9</i>		■	■	■						
<i>Pheidole sp. 10</i>							■			
<i>Procryptocerus batesi</i>				■		■				
<i>Procryptocerus mayri</i>				■						
<i>Pyramica urrhobia</i>			■							
<i>Rogeria foreli</i>					■					
<i>Rogeria sp. 1</i>		■								
<i>Rogeria sp. 2</i>		■								
<i>Sericomyrmex sp.</i>	■	■	■		■					
<i>Solenopsis sp. 1</i>			■		■	■	■	■		
<i>Solenopsis sp. 2</i>	■		■		■		■			
<i>Solenopsis sp. 3</i>	■	■	■							
<i>Solenopsis sp. 4</i>	■		■	■	■					
<i>Solenopsis sp. 5</i>				■						

